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Inducible Agonistic Structures in the Tropical Corallimorpharian, *Discosoma sanctithomae*

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Abstract. The Corallimorpharia are a group of soft-bodied anthozoans closely related to the scleractinian corals. Although numerous reports have documented the agonistic behaviors of actiniarians and hard corals, only Chadwick (1987) has shown such behaviors in a corallimorph (*Corynactis california*). The following investigation confirms the use of inducible aggressive structures in space competition in the laboratory and in the field by *Discosoma sanctithomae.* This tropical corallimorph used both modified marginal tentacles and mesenterial filaments to damage adjacent scleractinians. All colonies of *Agaricia agaricites* transplanted near *D. sanctithomae* were damaged. Initially, *D. sanctithomae* adjacent to *Meandrina meandrites* were severely wounded. However, 67% recovered and retaliated within a one to six month period, causing damage to *M. meandrina* that persisted for at least twelve months.

Introduction

Many benthic cnidarians that reproduce asexually expand their colonies proximally and radially. New individuals require space on the substrate to become established and to grow. In a coral reef environment, however, space is limiting, and as an individual, or clone, expands, competitive interactions are common. These competitive encounters may have provided important selective pressures for the evolution of agonistic behaviors and structures to deal with these competition events. Abel (1954) first described acrorhagi, the inflatable sacks around the collar of certain Actiniaria. Francis (1973a) noticed a particular spatial pattern among conspecific anemone clones of *Anthopleura elegantissima;* individuals of a clone were closely aggregated, but groups of different clones were always separated by an "anemone-free zone." This led Francis to describe a series of behaviors in which *A. elegantissima* used acrorhagi during agonistic interactions with non-clonemates. Other researchers have investigated various aspects of aggressive behavior in members of the class Anthozoa (Bonnin, 1964; Williams, 1975; den Hartog, 1977; Purcell, 1977; Bigger, 1980; Kaplan, 1983; Sammarco *et al.,* 1983; Bak and Borsboom, 1984; Hidaka and Yamazato, 1984; Sebens, 1984; Chadwick, 1987). Knowledge has evolved from initial descriptions of straightforward, predictable results of spatial competition events (Lang, 1971, 1973; Francis, 1973b; Chornesky, 1983; Chornesky and Williams, 1983) to descriptions of more complex, dynamic interactions. The importance of temporal scale was recognized, and many competitive outcomes were discovered to be reversible (Bak *et al.,* 1982; Logan, 1984; Chornesky, 1985). The initial victor was not always the ultimate winner. Other factors such as size, attack angle, and previous aggressive history affected the outcome of competitions (Brace and Pavey, 1978; Brace, 1981; Bak *et al.,* 1982). Also, significant work has been done elucidating the systems of recognition required for these agonistic behaviors (Theodor, 1970; Hildemann, 1974; Bigger, 1980; Sauer *et al.,* 1986). The number of species known to exhibit specialized structures used in aggressive behaviors has also increased, including members from four different orders within the class Anthozoa (reviewed by Lang and Chornesky, 1988).

In addition to acrorhagi, certain species in the order Actiniaria employ a modified feeding tentacle as a fighting tentacle (= catch tentacles, Purcell, 1977). Functionally similar to the acrorhagi, this elongated tentacle can adhere to neighboring non-clonemate conspecifics, causing tissue necrosis and ultimately, if successful, retreat of the opposition. As with *A. elegantissimma,* these behaviors have been reported to produce single-clone aggregates separated by anemone-free zones (Purcell, 1977; Purcell and Kitting, 1982). One report indicated the mechanism also worked

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on an intrasexual level, yielding anemone-free zones between clones of the same sex (Kaplan, 1983). Some scleractinians possess a structure similar to the actiniarians' fighting tentacle. Sweeper tentacles, so termed because they sweep the adjacent area, develop on polyps of certain reef corals (Richardson *et al.*, 1979; Chornesky, 1983; Chornesky and Williams, 1983; Hidaka and Yamazato, 1984). The development of sweeper tentacles is induced by the presence of, or aggression by, another coral (Chornesky, 1983). These interactions are primarily interspecific and are often used in conjunction with a second mechanism. Lang (1971, 1973) and Logan (1984) described the process of extracoelenteric digestion used by reef corals to avoid being overgrown and to acquire new space. The extrusion of mesenterial filaments through the mouth and body wall onto another coral results in partial mortality of the opposing colony.

Although the Octocorallia use allelochemicals in competitive interactions (Sammarco *et al.*, 1983, 1985; LaBarre, 1986; Pawlik *et al.*, 1987), until recently no member of this subclass was reported to have specialized structures used for aggression. Several reports described sweeper-like tentacles on species of Alcyonacea and Gorgonacea, but these tentacles are probably feeding apparati (Abel, 1970; Muzik, 1983). However, *Erythropodium caribaeorum* (Gorgonacea), develops sweeper tentacles and uses them for aggression (Sebens and Miles, 1988). These structures function in the same way as the sweeper tentacles of the scleractinians, but instead of only one or two tentacles per polyp becoming sweepers, all eight of the tentacles on many polyps elongate and are able to damage neighboring corals. It is of interest to note that *E. caribaeorum* is the only obligate encrusting gorgonian in the Caribbean. This growth form inevitably leads to interactions with a variety of other species requiring space on the primary substratum.

The Corallimorpharia are another order with members exhibiting agonistic behaviors. These soft-bodied members of the Hexacorallia resemble anemones, but are related more closely, morphologically and phylogenetically, to the scleractinians. Chadwick (1987) reported that the corallimorph *Corynactis californica* used mesenterial filaments against species of anemones and corals in agonistic interactions in the laboratory. Earlier, den Hartog (1977) described two types of tentacles along the rim of the oral disk of the corallimorph *Discosoma sanctithomae* (Duchassaing and Michelotti). Some of these marginal tentacles are thin and hair-like, whereas others are finger-like and bulbous. He found these bulbous tentacles to have larger and more dense holotrichous nematocysts than the thin counterparts and suggested that these might represent a morphological variant used in agonistic encounters, although no experimental work was done. Sebens (1976) examined this species in field and laboratory studies in Panama but found no evidence of agonistic behavior in short-term experiments. Here, I report the first field results demonstrating agonistic behavior in competitions between a corallimorph and several species of scleractinian corals. *D. sanctithomae* used both mesenterial filaments and enlarged marginal tentacles to damage the scleractinian corals *Agaricia agaricites* and *Meandrina meandrites*.

Materials and Methods

Site location and description

Field and laboratory experiments were completed at the Discovery Bay Marine Laboratory in Discovery Bay, Jamaica (18°30′N: 77°20′W). The reef crest along the north coast of Jamaica runs predominantly east to west, with spur and groove formations jutting out to the north. At Discovery Bay, the fore reef is separated from a well-developed lagoon by a conspicuous reef crest that has mounds of exposed coral rubble accumulated from Hurricane Allen in 1980. Spur and groove formations begin at 10 m on the fore reef and continue to the fore reef slope, which occurs at 21 m at some locations. The east back reef is predominantly a sandy bottom with *Thalassia* beds interspersed with patch reefs. Columbus Park is an area of the back reef with high concentrations of silt and of particulate matter that reduces visibility. Shallow areas are dominated by benthic soft-bodied zoantharians within a dead *Acropora cervicornis* framework. The deeper regions possess a rich sponge and mollusk community. For a more detailed description, see Goreau (1959), Goreau and Goreau (1973), and Liddell *et al.* (1984). Survey data were collected from the west back reef and Columbus Park, and from Long Term Study (LTS), Kinzie's Reef, and Lynton's Mine on the fore reef. Transplant experiments were located at all the fore reef survey sites between depths of 10 m and 20 m (Fig. 1).

Animal descriptions and collection

Discosoma sanctithomae is a corallimorpharian common throughout the Caribbean and Bermuda between depths of 1–20 m (den Hartog, 1980). Both solitary individuals and asexually produced clonal aggregates can be found living within the coral reef framework. The animal is orally-aborally flattened, with the oral disk averaging approximately 4 cm in diameter (Fig. 2A). A margin at the edge of the oral disk lacks tentacles and is often tucked up under the disk, but at other times is expanded well beyond the basal attachment area. The oral disk tentacles of *D. sanctithomae* are very short, stubby, and are often ramous. A second group of tentacles extends radially from the margin of the disk and are thus termed marginal tentacles.

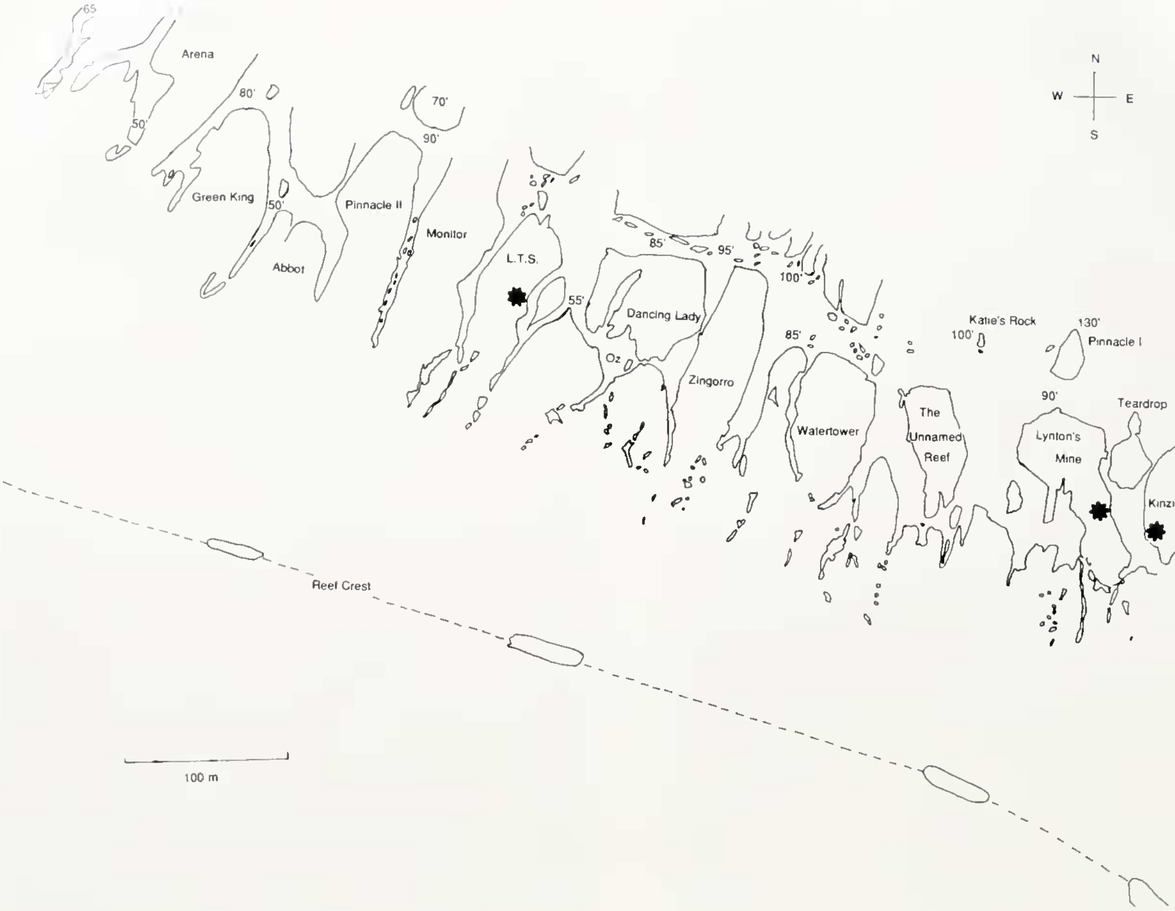

Figure 1. Map of the fore reef at Discovery Bay, Jamaica. Areas marked with stars indicate sites of transplant experiments and fore reef survey sites.

Specimens of *Discosoma sanctithomae* used in the field experiments were never removed from the reef or disturbed in any way. Individuals were identified by tags placed on nearby coral rubble. *D. sanctithomae* used in laboratory experiments were collected along with pieces of the substrate, usually dead *Acropora cervicornis*, because attempts to scrape off individuals were always unsuccessful. The collected animals were placed in a running seawater table and allowed to acclimate for three to seven days before being used in experiments.

The scleractinian corals *Agaricia agaricites* (Pallas) and *Meandrina meandrites* (L) were used in the field transplants. Pieces of coral (approximately 6 × 8 cm) were collected using a rock hammer and chisel to release them at their base or at an area of dead coral skeleton. The corals were collected from the same reefs onto which they were to be transplanted. They were not brought to the surface, but were left for two to seven days before being transplanted. Corals were not used if they showed signs of tissue damage from the collection methods within this period. *A. agaricites* and *M. meandrites* used in the laboratory experiments were collected in a similar manner. However, these corals were transferred to running seawater tables and allowed to acclimate for three to seven days.

Field surveys

Field surveys of *Discosoma sanctithomae* were conducted to determine which organisms lived adjacent to the corallimorph and what interactions were occurring. The surveys were done by swimming parallel transects across depth contours throughout a designated area and recording every *D. sanctithomae* observed. Each of the *D. sanctithomae*'s neighbors were noted, and any damage on either *D. sanctithomae* or any neighbor was recorded. Percent-cover data were gathered from the same area as the *D. sanctithomae* survey. Survey procedures involved assigning random numbers to a chain-link transect that was haphazardly dropped within the study area. Species or substrate type that fell under each of the marked chain links was recorded (Rogers *et al.*, 1983). Information from

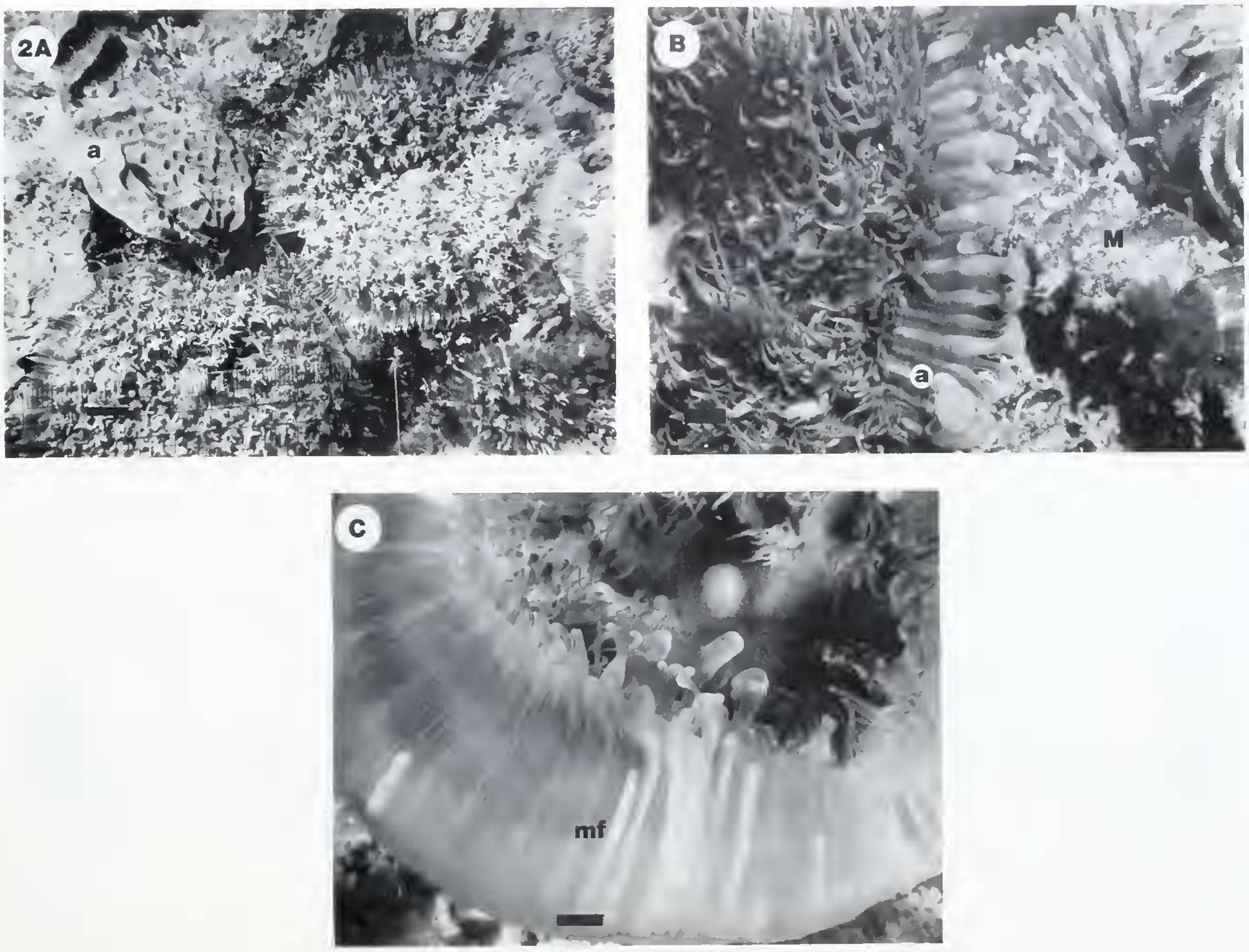

Figure 2. (A) *Agaricia agaricites* (a) transplanted next to a *Discosoma sanctithomae* with thin marginal tentacles (arrows). Scale = 1 cm. (B) *D. sanctithomae* adjacent to *Meandrina meandrites* (M) developed large swollen acrospheres (a) at the tips of the marginal tentacles. Areas of the rim have become enlarged also. Scale ≈ 2 mm. (C) *D. sanctithomae* with acrospheres. Mesenterial filaments (mf) can be seen in the area of the coelenteron leading to the marginal tentacles. Scale ≈ 2 mm.

the *D. sanctithomae* survey and the percent cover transects was compared to determine whether *D. sanctithomae*'s contact with neighbors was random or reflected some sort of selection for, or by, neighboring species.

Transplant experiments

Field. Manipulative experiments were done in the field to study the interactions of *Discosoma sanctithomae* and scleractinian corals. Pieces of coral were epoxied adjacent to, but not touching, individual *D. sanctithomae,* which were partially retracted. However, transplants were located so that fully expanded *D. sanctithomae* would touch the coral's tissue. The Pettit Underwater Patching Compound used to fix the corals in place was not toxic when applied only to the dead base of the coral. Corals showing a general tissue necrosis (possibly from handling) soon after the transplant (1–2 days) were removed from the study; this accounts for most of the discrepencies between initial and final sample sizes. Specific sets of transplants were designed to address the following questions: (1) Can *D. sanctithomae* damage scleractinian corals adjacent to them? (2) Are bulbous marginal tentacles with acrospheres associated with the damage to corals? (3) Do *D. sanctithomae* react differently depending on the species of coral that is next to them?

Three sets of transplants (Series I) were begun in January 1987. In the first set of transplants (T1) pieces of *Agaricia agaricites* (n = 19) were placed next to *D. sanctithomae* with filiform marginal tentacles (Fig. 2A). A second group of transplants (T2) paired *A. agaricites* (n = 16) with *D. sanctithomae* that had bulbous marginal tentacles. *A. agaricites* was chosen because it was found frequently next to *D. sanctithomae* in the field surveys. Both sets of transplants were designed to examine *D. sanctithomae*'s tendency to damage corals. Also, if the bulbous tentacles were responsible for damage to the scleractinians, the corals in T2 would be expected to incur damage more quickly than the corals in T1. *Meandrina meandrites* (n = 18) was used in a third transplant experiment (T3) to test for any variation in response by *D. sanctithomae*. Unlike *A. agaricites*, this coral is known to use mesenterial filaments readily in aggressive encounters (Lang, 1973; Logan, 1984). All experimental pairs were monitored for damage to *D. sanctithomae* or to *A. agaricites*, and for any changes in the morphology of the marginal tentacles on *D. sanctithomae* once a week for five weeks, again after five months, then after one year. Several night dives were done to confirm damage to coral polyps and to check for development of sweeper tentacles (Chornesky, 1983). Photographs of experimental pairs were taken weekly with a Nikonos camera with a 2:1 extension tube, and a Minolta XL401 Super-8 movie camera was left on the reef for four days at a time, taking photographs at 1.5-min intervals. A second series of transplants (Series II) was started in February 1988. These experiments were identical to the 1987 T1 and T2 transplants except that they were monitored once a day for two and a half weeks to examine the interactions over a shorter time period.

Two types of controls were used to test for the effects of the transplantation process. Pieces of coral transplanted near *Discosoma sanctithomae* were always large enough so that at least half of their tissue area was out of reach of the *D. sanctithomae*, even when fully expanded (opposite-side controls). Additional pieces of coral were transplanted among the experimental pairs, but not within reach of any *D. sanctithomae*. These corals were regularly examined for any signs of damage. A control for *D. sanctithomae* acrosphere formation was done by observing the marginal tentacles of two sets of *D. sanctithomae* that were surrounded only by algae. One group of *D. sanctithomae* was monitored once every ten days for two months. The second group was monitored every day for up to twenty days. These individuals were studied to determine whether sporadic changes in the marginal tentacles occurred without contact with cnidarian neighbors.

Laboratory experiments. Transplant experiments similar to those in the field were done in the laboratory in running seawater tables. *Discosoma sanctithomae* individuals were paired with pieces of *Agaricia agaricites* (n = 5) and *Meandrina meandrites* (n = 5). None of the *D. sanctithomae* had enlarged marginal tentacles, nor did the corals have sweeper tentacles at the beginning of the experiment. When both members of an experimental pair were contracted, neither touched the other. Three pieces of *A. agaricites* and two of *M. meandrites*, as well as three individuals of *D. sanctithomae*, were out of reach of any other anthozoan and acted as the controls. These pairs were inspected for damage every hour for the first seven hours. Throughout the experiment a Super-8 movie camera with an intervalometer photographed individual pairs every 1.5 min. The experiment continued for eight days.

Results

Survey data

The neighboring species of more than 155 *Discosoma sanctithomae* were recorded (Fig. 3A, B). Approximately 37% (n = 238) of them were foliose or turf complex algae, the largest group total. The second most common group found adjacent to *D. sanctithomae* were crustose coralline

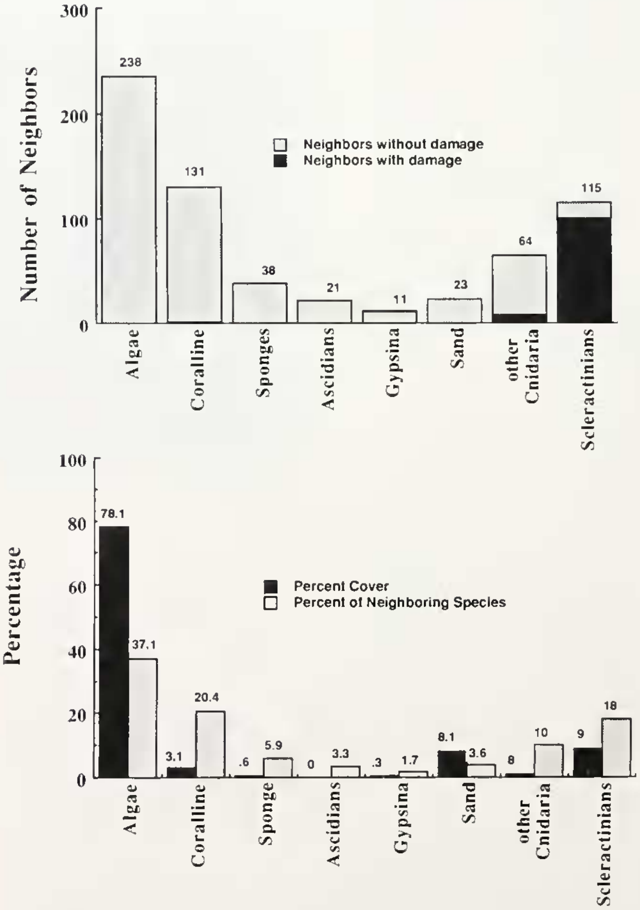

Figure 3. (Top) The area adjacent to individual *Discosoma sanctithomae* were surveyed at all transplant sites on the fore reef and in Columbus Park. Neighboring species and substrate type were counted and classified as damaged or not damaged; exact counts are reported above bars. Each organism and substrate type counted as "1" interaction regardless of size; this may underestimate the impact of larger organisms and overestimate those of smaller ones. (Bottom) Surveys of species percent-cover were done at all the neighbor survey sites. Sixteen transects were completed: 713 chain-link transect points were classified into the same eight catagories used for the neighbor survey. Numbers above each bar represent percentages for each group. Percent-cover results (black) are compared to percentage data of neighboring species (white; n = 641).

algae (20.4%), followed by the scleractinian corals (18%). The corals found most frequently adjacent to the corallimorphs were *Montastrea annularis*, *Siderastrea siderea*, and *Agaricia agaricites*. In more than 75% of the cases when *D. sanctithomae* was adjacent to a scleractinian, there were areas of dead coral associated with the area of contact. Damage was not readily apparent in any other group (Fig. 3A).

Although algae were also the most abundant organisms in the surveys of percent cover (n = 557, 78%), scleractinian corals (9%) and sand (8%) were the second and third most commonly occurring items, respectively (Fig. 3B). The complement of species and groups neighboring *D. sanctithomae* proved to be significantly different than the proportion of species expected from the percent cover survey using a G-test for independence (G = 21.03, $P < 0.05$). Algae have been dominant space occupiers in the fore reef community since the die-off of *Diadema antillarum* in 1983 (Liddell and Ohlhorst, 1983).

Field transplants

Series I. Sixteen of seventeen *Discosoma sanctithomae* originally with filiform tentacles had developed bulbous tentacles with acrospheres in the presence of *Agaricia agaricites* within six weeks. The mean time for acrosphere development was 17.3 ± 2.0 days (mean ± S.E.). During this time, all 17 of the *A. agaricites* colonies had been damaged; the mean time to damage from each colony was 17.9 ± 1.8 days (mean ± S.E.) (Fig. 4A). In comparison, only one opposite-side control was damaged. Formation of acrospheres and the occurrence of damage was significantly greater than that which might occur by chance (G-test with William's correction factor: G = 15.5; G = 23.0 resp.; $P < 0.05$). The time to acrosphere development was not significantly different from the average time for damage to occur to the corals (Mann-Whitney: U′ = 170.5, $P < 0.05$).

All 12 *Agaricia agaricites* colonies placed next to the *Discosoma sanctithomae* that had acrospheres at the start of the experiment (T2) were damaged. The average time to damage (10.0 ± 1.7 days, mean ± S.E.) was significantly faster than the time to damage for the transplants that later formed acrospheres (T1) (Mann-Whitney: U = 204, $P < 0.05$) (Fig. 4A). Again, only one opposite-side coral control was damaged. Sweeper tentacles on *A. agaricites* occurred on only one colony. They formed after the interactions had progressed for about one month and after the coral had been initially damaged by the corallimorph. The corresponding *D. sanctithomae* did not reveal any damage.

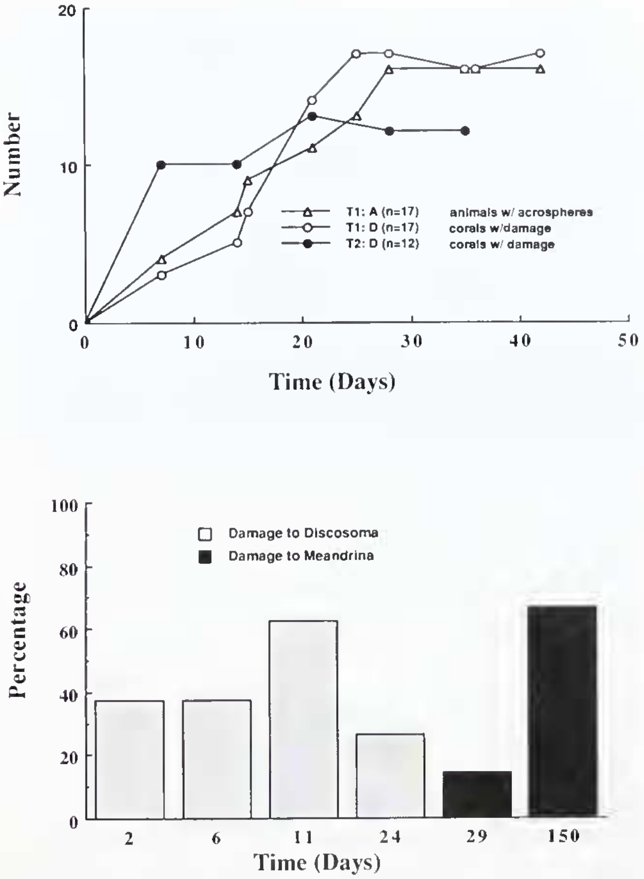

Figure 4. (Top) Results of two field transplant experiments (T1 & T2) are shown. In the first transplant (T1) 17 corals were placed next to *Discosoma sanctithomae* with thin marginal tentacles. T1:A (△) charts the progression of acrosphere development in *D. sanctithomae*. T1:D (○) tracks the development of damage to the corals. In T2, 12 corals were next to *D. sanctithomae* that possessed acrospheres. T2:D (●) records the damage incurred to the adjacent corals. (Bottom) Results of field transplant 3 (T3). Eighteen *Meandrina meandrites* were placed near *D. sanctithomae* with acrospheres. Initially 38% of the *D. sanctithomae* were severely injured; two died within the first month. Although none of the corals suffered damage before the end of the first month, 67% of the remaining transplants were damaged over the subsequent six-month period and remained damaged for at least twelve months.

The results of the *Discosoma sanctithomae* transplants with *Meandrina meandrites* were strikingly different. Within one week, 38% of the *D. sanctithomae* (n = 16) had suffered severe body lesions from the mesenterial filaments of *M. meandrites* (Fig. 4B). This increased to 63% within two weeks, culminating in the death of two *D. sanctithomae* individuals within the first month. The first incidence of damage to *M. meandrites* did not occur until almost one month had passed. However, of those *D. sanctithomae* that survived the first two months (n = 12), 67% went on to damage the *M. meandrites* over the next four months. Damage inflicted by these *D. sanctithomae* was still visible twelve months later (Fig. 5). None of the opposite-side coral controls were damaged.

Series II. Results of the Series II transplants were similar to Series I results. Ten of eleven *A. agaricites* corals placed

Figure 5. *Discosoma sanctithomae* vs. *Meandrina meandrites:* interaction after twelve months. Note the large acrospheres (a) and the algae-covered dead coral skeleton (d). Live coral polyps (p) can be seen out of reach of the *D. sanctithomae*'s tentacles. Scale ≈ 2.7 mm.

next to *Discosoma sanctithomae* with acrospheres were damaged in 12.0 ± 1.5 days (mean ± S.E.). Only two of the eleven corals adjacent to *D. sanctithomae* without acrospheres were clearly damaged (6.0 ± 5.0 days, mean ± S.E.). Only three of eleven had developed acrospheres within the trial period of 10 to 20 days. This short period before damage occurred reflects one coral that was extensively damaged after the second day by mesenterial filaments that were released through the marginal tentacles of the corallimorph. Mesenterial filaments were observed being extruded by *D. sanctithomae* through the tentacles on numerous other occasions, and were extruded frequently from the mouth and through the body wall as well.

Controls

None of the isolated coral controls experienced any tissue damage. The lack of incidences of damage to opposite-side coral controls were reported with the results for the particular transplant. The *D. sanctithomae* individuals acting as controls for random acrosphere development showed little change; no acrospheres were formed. There were, however, frequent influxes and effluxes of mesenterial filaments to and from the marginal tentacles. At times the filaments remained between the mesenteries in the coelenteron, and at other times they traveled into the tips of the marginal tentacles.

Laboratory experiments

The results of the laboratory experiments were a brief accelerated version of the field experiments. All the corals, and the *Discosoma sanctithomae* individuals, retracted their polyps when the experimental pairs were initially established. Although eight of ten corals partially expanded their polyps within 20 min, and all the *D. sanctithomae* adjacent to *A. agaricites* had relaxed within the first hour, there was no direct contact. The *D. sanctithomae* next to the *M. meandrites* remained contracted, with four of them extruding mesenterial filaments within the first seven hours.

Meandrina meandrites transplants were equally active. All five corals released mesenterial filaments onto the *Discosoma sanctithomae* within the first 7 h. *D. sanctithomae* near *A. agaricites* also extruded filaments but, in general, the severity of such attacks was greatly reduced compared to those with *M. meandrites.* Within 24 h, 4 *D. sanctithomae* had mucus layers covering body wounds inflicted by *M. meandrites'* mesenterial filaments. Body postures were strongly evasive, especially when compared to *D. sanctithomae* near *A. agaricites;* the latter often laid their marginal disks over the coral surfaces. By the end of the third day, four of the five corallimorphs near *M. meandrites* were dead. The fifth had severe body lesions and had partially released its hold on the substrate. None of the *M. meandrites* individuals were damaged.

None of the *Agaricia agaricites* individuals were observed releasing mesenterial filaments, nor using sweeper tentacles. A general pattern evolved for the *D. sanctithomae-A. agaricites* interactions of gradual expansion of the *D. sanctithomae* onto the coral's surface followed by retraction, and intermittent extrusion of mesenterial filaments by *D. sanctithomae. Discosoma sanctithomae* was able to damage *A. agaricites* in two separate cases, although the coral recovered its damaged area in one of these events. Three *D. sanctithomae* adjacent to *A. agaricites* died within eight days, but two of these deaths must be qualified. Two of the fatalities resulted from the *D. sanctithomae* releasing its hold near the *A. agaricites* and wandering into a colony of *M. meandrites.* None of the *D. sanctithomae* individuals formed marginal tentacles. All the control corals survived without damage, and one of the three control *D. sanctithomae* individuals died.

Discussion

Although lacking a hard skeleton, the soft-bodied relatives of the scleractinians, such as the Actiniaria, have proven to be able competitors for space (Francis, 1973a; Purcell, 1977; Purcell and Kitting, 1982; Chadwick, 1987). More recently, investigators have discovered that the Corallimorpharia possess aggressive abilities as well. During prolonged interspecific exposure, *Corynactis californica* killed polyps of the actiniarians *Anthopleura elegantissima* and *Metridium senile,* as well as the scleractinians *Astrangia lajollaensis* and *Balanophyllia elegans* by extruding mesenterial filaments (Chadwick, 1987). The present study supplies evidence that another corallimorph, *Discosoma sanctithomae,* can compete successfully with scleractinian corals for primary space. Every colony of *Agaricia agaricites* transplanted next to *Discosoma sanctithomae* was damaged, whereas none of the associated *D. sanctithomae* were damaged. Most of the damage occurred within the first month of a 14-month experimental period. *D. sanctithomae* was able to cause severe necrosis of tissue on the coral *Meandrina meandrites,* which is considered to be near the top of the Caribbean coral competitive hierarchy due to its effective use of mesenterial filaments in damaging other scleractinians (Lang, 1973). Although many of the *D. sanctithomae* were initially inflicted with extensive body lesions by *M. meandrites,* many recovered and retaliated successfully, causing damage that persisted at least twelve months. This represents a clear and dramatic example of a competitive reversal and places *D. sanctithomae* near the top of a zoantharian competitive hierarchy.

Most of the agonistic behaviors of soft-bodied anthozoans (and some scleractinians) involve morphological modifications that provide the capability to inflict damage. Anemones in the family Actiniidae inflate acrorhagi (Abel, 1954; Francis, 1973a; Sebens, 1984); acontiate anemones in several families develop "fighting tentacles" from feeding tentacles (Purcell, 1977; Purcell and Kitting, 1982; Kaplan, 1983). *D. sanctithomae* uses marginal tentacles frequently filled with mesenterial filaments and ectoderm engorged with specialized nematocysts (den Hartog, 1977, 1980). The marginal tentacles changed from thin, filiform appendages to bulbous acrospheres in the presence of *A. agaricites* and *M. meandrites.* The initial increase in volume seems to be due to the influx of mesenterial filaments, which is later compounded by the ectoderm thickening with nematocysts (as seen by den Hartog, 1977). Unlike the acrorhagi (Bonnin, 1964; Bigger, 1980), which become inflated with each aggressive interaction, the marginal tentacles of *D. sanctithomae* remain bulbous once enlarged. In this study, the most extensive acrospheres were found closest to the site of interaction with the scleractinians. Acrospheres never developed in *D. sanctithomae* surrounded only by algae, nor were they found in *D. sanctithomae* adjacent to sponges, tunicates, or other non-cnidarian neighbors in the field surveys.

Every incidence of damage to the experimental corals was associated with the presence of acrospheres except in one case. The association between acrospheres and damage is further supported by a decrease in the amount of time before damage appeared on the corals next to *D. sanctithomae* with acrospheres compared to those that developed acrospheres during the experiment. As the interactions progressed, algae may have acted as a buffer to contact with the acrospheres. After algae began to settle on the bare coral skeleton, the acrospheres did not intensify further.

Discosoma sanctithomae responded to the corals adjacent to them by developing acrospheres and by inflicting damage. However, the response was extremely graded. *D. sanctithomae* reacted to *Agaricia agaricites* much differently than it did to *Meandrina meandrites.* In general, the interactions with *A. agaricites* appeared to be much more gradual, progressing slowly, but ultimately resulting in the development of acrospheres on *D. sanctithomae* and damage to the coral. Conversely, the behavior of *D. sanctithomae* next to *M. meandrites* was much more dramatic, responding to the aggressive actions of *M. meandrites.* Within less than twenty-four hours, *D. sanctithomae* individuals had been damaged extensively and were withdrawn, some for several days. Those that later recovered and attacked *M. meandrites* did so with well-developed acrospheres. Often the marginal tentacles and even the rim of the oral disk were thickened and swollen (pers. obs.), presumably filled with potent nematocysts (den Hartog, 1977) (Fig. 2B).

The laboratory experiments and the Series II transplants served to elucidate the differences in *Discosoma sanctithomae*'s behaviors. *D. sanctithomae*'s response to adjacent *Meandrina meandrites* was immediate and severe. *M. meandrites'* quickness in extruding mesenterial filaments and inflicting damage deterred *D. sanctithomae* from approaching *M. meandrites.* In contrast, *D. sanctithomae* placed next to *Agaricia agaricites* repeatedly relaxed and expanded its disk directly on top of *A. agaricites'* living tissue. *D. sanctithomae* did not appear to be adversely affected by *A. agaricites,* although it did periodically retract away from contact with the coral. *D. sanctithomae* could cause small amounts of necrosis to *A. agaricites'* tissue which, at least in the early stages, was often recovered by the coral. However, sometime after prolonged exposure and repeated attacks, the *A. agaricites* was no longer able to regain lost tissue. Not long after this stage, algae (usually a green alga) began to settle on the bare coral skeleton. These dead areas persisted for the remainder of the study period.

The use of mesenterial filaments in competitive interactions is well documented for scleractinians. Some of the most aggressive corals use exclusively mesenterial filaments for defense (Lang, 1971, 1973; Logan, 1984). The corallimorph *Corynactis californica* extruded mesenterial filaments primarily out the mouth but also through the body wall and once through the tentacles during agonistic encounters (Chadwick, 1987). *Discosoma sanctithomae* invoked two mechanisms for inflicting damage that reflect its phylogenetic relationship with the scleractinians and its particular tentacle morphology. Like many hard corals, the corallimorph readily emitted mesenterial filaments out of the mouth and through the body wall when disturbed.

In addition, *D. sanctithomae* continually transferred mesenterial filaments into the discal and marginal tentacles, sometimes passing them out through the tips. It is not yet known whether there are permanent holes at the tips of these tentacles through which the mesenteries can pass. A similar movement of mesenterial filaments occurs in the discal tentacles of *Rhodactis howesii* (Corallimorpharia) during feeding behaviors (Hamner and Dunn, 1980).

This regular fluctuation of mesenterial filaments dispose *Discosoma sanctithomae* to be capable of quickly sending mesenterial filaments into and out of the tips of the marginal tentacles when it is involved in agonistic encounters with neighboring species. *D. sanctithomae* was observed to damage adjacent corals with mesenterial filaments from its marginal tentacles. Although most incidences of damage occurred after acrospheres had formed, some corals showed damage before this time that could have been caused by mesenterial filaments. By extruding the filaments out the tips of the marginal tentacles, *D. sanctithomae* increases the probability of the filaments landing on the tissue of the opposing organism. It is a behavior that the corallimorph can invoke quickly at the time of interaction because mesenterial filaments regularly fluctuate in and out of the marginal tentacles. Hence, there is less time between the recognition of a competitor and the commencement of an aggressive response than would be required to form sweeper or fighting tentacles.

Den Hartog (1977) determined that the size and density of holotrich nematocysts was greater in bulbous marginal tentacles than in the filiform type. This study confirms that interactions with scleractinians can induce the formation of bulbous tentacles. After a period of less than a week, thin transparent marginal tentacles of *Discosoma sanctithomae* became thickened and more opaque in the presence of the coral colonies. Some tentacles doubled in thickness and became opaque, while others more than tripled their girth and were associated with a greatly thickened oral rim. A few tentacles elongated, forming distinct tips with acrospheres (Fig. 2). All forms of these thickened marginal tentacles were able to cause necrosis of the coral tissue.

The combination of mesenterial filaments and acrospheres enabled *D. sanctithomae* to respond immediately, warding off imminent damage, and to develop an alternate form of defense that required more time to initiate. *D. sanctithomae* may use mesenterial filaments in response to adverse interactions of short temporal scale, and reserves acrosphere formation, involving the costly construction of new tissue and many nematocysts, for prolonged interactions. Its soft body allows it to avoid some acts of aggression from opponents by bending away and perhaps even by moving the base laterally. All such characteristics make *D. sanctithomae* an effective competitor, holding its own on the substratum of the reef against some of the most aggressive corals.

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